Beyond Climate Envelope Projections: Roe Deer Survival and Environmental Change

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ABSTRACT Research on climate change impacts has focused on projecting changes in the geographic ranges of species, with less emphasis on the vital rates giving rise to species distributions. Managing ungulate populations under future climate change will require an understanding of how their vital rates are affected by direct climatic effects and the indirect climatic and non-climatic effects that are often overlooked by climate impact studies. We used generalized linear models and capture–mark–recapture models to assess the influence of a variety of direct climatic, indirect climatic, and non-climatic predictors on the survival of roe deer (*Capreolus capreolus*) at 2 sites in Sweden. The models indicated that although direct climatic effects (e.g., precipitation) explained some variation in survival, indirect climatic effects (e.g., an index of vegetation production), and non-climatic effects (hunting by lynx [*Lynx lynx*] and humans) had greater explanatory power. Climate change is likely to increase vegetation productivity in northern Europe, and, coupled with the positive effects of vegetation productivity on roe deer survival, might lead to population increases in the future. Survival was negatively affected by lynx presence where these predators occur and by human harvest in the site that lacked predators. In the future, managers might find that a combination of increased harvest and predation by recovering carnivore populations may be necessary to mitigate climate-induced increases in roe deer survival. Considering vegetation availability and predation effects is likely to improve predictions of ungulate population responses to variation in climate and, therefore, inform management under future climate change.

Research into the impacts of climate change on biodiversity has focused on identifying areas where wildlife could find suitable climate in the future, without considering how well populations would perform in the climatically suitable areas that are identified (Araujo and Guisan 2006, Thuiller et al. 2006, Huntley et al. 2008, Elith and Leathwick 2009). Species distribution models used to determine these climate envelopes generally assume that species are in equilibrium with their environment thereby ignoring the dynamic processes underlying species ranges (Guisan and Thuiller 2005, Pagel and Schurr 2012). Such models often are of little practical use to wildlife managers whose decisions are generally site specific and focus on population abundance and viability rather than simple occurrence. Filling this gap requires mechanistic models of population dynamics that can project population growth within climate envelopes to inform management decisions (Barnard and Thuiller 2008, Huntley et al. 2010, Dormann et al. 2012). The vital rates that determine population growth (i.e., survival, reproduction, dispersal) are influenced by a wide range of climatic and non-climatic factors that might operate via complex pathways (Forchhammer et al. 2002, Wang et al. 2002). Population models that incorporate this complexity will provide useful insight into how climate change will influence the management of wildlife populations.

Ungulate populations typically demonstrate complex, age-structured population dynamics influenced by direct climatic, indirect climatic, and non-climatic factors (Gaillard et al. 2000b, Sinclair and Krebs 2002, Owen-Smith 2010, Mysterud and Sæther 2011), providing useful systems for examining different drivers of survival simultaneously. For example, populations experiencing increased survival due to milder winters (i.e., direct effect through reduced energy expenditure) might also experience increased survival because of climate-related increases in vegetation productivity (i.e., indirect effect; Mysterud and Ostbye 2006). In many ungulate populations, the relatively non-climatic impacts of predation and hunting can further complicate the survival component of population growth. Including predation and hunting in models of climatic impacts on survival is crucial because they can obscure relationships between survival and climate and can be managed to reduce fluctuations of ungulate populations (Sinclair 1997, Ballard et al. 2001, Apollonio et al. 2010). Natural predation and hunting by humans can mitigate climate change impacts by reducing variation in population growth and vital rates, thereby dampening the fluctuations of prey populations (Wilmers et al. 2006, 2007; Gilg et al. 2009). Only by simultaneously considering the effects of climate, climate-related changes in food resources, predation, and human management can researchers develop survival models to underpin mechanistic simulations of population growth and inform effective management plans in the face of climate change.

Collecting the data to address the complex pathways influencing population dynamics poses a considerable challenge. Several long-term datasets on ungulates have furthered the understanding of population dynamics (Clutton-Brock et al. 1985, Gaillard et al. 1993, Coulson et al. 2001). Yet, most of these studies come from sites without predators or human harvest, thus omitting 2 potential influences on survival that affect many

ungulate populations (Gaillard et al. 2000b, Nilsen et al. 2009a). Additionally, studies addressing climate-influenced population dynamics in ungulates often suggest that lagged effects of climate are mediated by altered vegetation production (Forchhammer et al. 1998, Wang et al. 2002, Griffin et al. 2011), without including explicit vegetation measures to examine this link.

The European roe deer (Capreolus capreolus) provides an excellent study species for evaluating the role of climate and other factors in determining ungulate vital rates. A multitude of factors could potentially influence roe deer mortality. Studies of roe deer repeatedly suggest that winter is the critical period for survival, with harsh climate conditions increasing mortality (Fruzinski and Labudzki 1982, Cederlund and Lindström 1983, Gaillard et al. 1998). In particular, snowfall has been identified as important because deep snow impedes mobility and restricts access to ground vegetation, leading to starvation (Cederlund 1982, Fruzinski and Labudzki 1982, Mysterud et al. 1997, Mysterud and Ostbye 2006). Inter-annual variation in net primary production of vegetation (NPP) could be important also; food availability throughout the year may contribute to body mass accumulation, which can affect winter survival (Gaillard et al. 1998, 2000a; Pettorelli et al. 2006). This possibility is consistent with studies linking higher NPP to higher population densities and growth rates of roe deer (Melis et al. 2009, 2010). Finally, hunting by humans and predation by lynx (Lynx lynx) are likely top-down influences on roe deer mortality. Roe deer were almost extirpated from much of Europe because of hunting (Randi 2005) and continue to be managed using annual hunting seasons (Apollonio et al. 2010) that can modify generation times and consequently population dynamics (Nilsen et al. 2009a). Lynx specialize on roe deer, commonly killing adults and maintaining high kill rates even when roe deer densities are low (Aanes et al. 1998, Nilsen et al. 2009b, Mejlgaard et al. 2013). Despite awareness of these various factors, analyses of roe deer survival generally have been limited to a small subset of possible variables and have emphasized hypothesis testing rather than building more comprehensive models that could be used to simulate population dynamics.

In addition to the theoretical incentives, roe deer population growth has important management implications. Recent increases in roe deer populations are associated with large economic costs from vehicular collisions, and damage to commercial forests and crops (Cederlund et al. 1998) but also contribute to recreation-based economies (e.g., hunting). Climate change has been suggested as a possible cause of further roe deer population growth (Melis et al. 2009). Estimates of climate-related effects on roe deer survival and of the potential for controllable non-climatic factors (e.g., hunting) to counteract those effects would be of practical use to managers.

We used data from 2 sites in Sweden with long-term, individual based, roe deer monitoring programs to investigate the importance of non-climatic, direct, and indirect climatic influences on survival rates. The 2 study sites examined provide a useful comparison between an inland site with harsh winters and large predators (i.e., Grimsö)

and a coastal site with milder winters and no large predators (i.e., Bogesund). Specifically, our objectives were to evaluate the importance of climatic conditions for variation in annual roe deer survival and determine if explicit inclusion of indirect climatic (e.g., vegetation) or non-climatic (e.g., human harvest and predation) predictors improve models of roe deer survival.

STUDY AREA

Bogesund is situated in the Stockholm Archipelago and covered by mixed coniferous-deciduous forest and farmlands (Fig. 1). Bogesund's landscape is characterized by broad valleys intersected by low ridges and elevation ranging from 0 m to 60 m above sea level. The warmest month is July (mean temp. 18.78 C) and the coldest is January (mean temp. 3.78 C). Annual precipitation is approximately 55cm. Snow cover lasts approximately 80 days from late December to early March (Swedish Meteorological and Hydrological Institute 2015). The only natural predator in Bogesund is the red fox (*Vulpes vulpes*), which preys only on fawns (Aanes et al. 1998, Jarnemo and Liberg 2005). Roe deer populations in Bogesund have been intensively managed, including a controlled density manipulation study from 1988 to 1994. In 1988, the Bogesund site was divided into a western experimental area (12.5 km^2; Fig. 1c) and an eastern control area (13.5km^2; Kjellander 2000). We used data from the more closely monitored population in the experimental area (hereafter the study area), where human harvest was halted from 1988 until the 1992–1994 period when >300 deer were culled (about 75% of the population; Kjellander 2000). After 1994, harvests varied but were moderate allowing the density to recover and become relatively stable.

The Grimsö site is an 80-km^2 area within the Grimsö Wildlife Research Area (GWRA; Fig. 1b) approximately 150km northwest of Bogesund and consists primarily of coniferous forest interspersed with bogs, mires, and fens. Grimsö's landscape is fairly flat with elevation rising gradually from 75 m in the south to 180 m above sea level in the north. Roe deer in Grimsö have been loosely managed since the 1970s with the goal of allowing natural processes (e.g., climate, predation, density-dependence) to regulate the population. Throughout the study, managers of the GWRA allowed deer hunting that helped limit population growth without decreasing abundance. The warmest month is July (mean temp. 18.88C) and the coldest is January (mean temp. 1.38C). Annual precipitation is approximately 67 cm. Snow normally covers the ground for 130 days from November to April, but inter-annual variation is pronounced (Swedish Meteorological and Hydrological Institute 2015). Grimso€ is inhabited by red fox, wolves (Canis lupus), and lynx. The area was colonized by a single wolf pack in 2003; from 2003 to 2010 the pack averaged 4.00 ± 2.73 individuals (mean ± SD; Wabakken et al. 2001, 2011). Tracks of a lynx family were first observed in Grimsö in 1996. Regional estimates suggest an average of 2.44 ± 0.65 lynx family groups/ 1,000 km^2 from 1994 to 2006 (Andr_en et al. 2002).

METHODS

Deer Monitoring

Researchers from the Swedish University of Agricultural Sciences (SLU) captured deer using box traps each winter since 1988–1989 in Bogesund (Fig. 1c; Kjellander 2000) and 1973–1974 in Grimsö (Fig. 1b); however, we use data only from 1985 onward in Grimsö, avoiding earlier years when a majority of radio-collared individuals were shot to retrieve collars. During the study, researchers baited traps with livestock forage pellets in the evening and checked traps the following morning. They kept few records on the frequency of trapping at either site so we calculated the sum of unique capture dates achieved each winter as an index of trapping effort.

Researchers marked captured deer using ear-tags with unique identification (ID) numbers and colors and, when possible, fitted them with radio-collars (Televilt International, Lindesberg, Sweden; Kjellander 2000). They estimated age of individuals based on tooth eruption, tooth wear, and body characteristics (Cederlund et al. 1991). Data on young fawns (<4 months) were not collected for most of the study period and the determinants of fawn survival can be very different from those affecting older deer (e.g., predation; Aanes et al. 1998, Linnell et al. 1998), so we excluded summer fawn records (from May to Sep). The marking and handling of roe deer were approved by the Ethical Committee on Animal Experiments, Uppsala, Sweden (Current approval Dnr: C302/2012).

Live observations came from various sources. Many deer were recaptured in box traps in winter (Debeffe et al. 2015). Additionally, researchers located radio-collared individuals at least once a month throughout the year and up to once a week during the winter. Over the years, 38 ± 16.2% (mean ± SD) of the deer at Bogesund have been collared; for Grimsö this percentage is unknown. Further records were obtained by researchers conducting routine fieldwork who recorded the date, location, and ID of any deer observed.

Records of deaths of marked individuals also come from 3 sources: inactive radio-collared deer, hunters' reports of deer harvested, and dead deer found incidentally by researchers or visitors. We recorded obvious causes of death (e.g., harvested) and if the body was emaciated, we recorded the cause of death as natural. If there were signs of predators at the death sites and no other cause was implicated, we classified cause of death as likely predation. Finally, if there was mixed evidence for the cause of death, we recorded it as unknown.

Researchers estimated deer density in Bogesund every April and September from 1989 to 2006 (Kjellander et al. 2006) using the Lincoln–Petersen method (Caughley 1977). In Grimsö, researchers estimated roe deer density each April since 1977 using pellet counts (Lindström et al. 1994). The original sampling grid included approximately 440 sampling plots (10 m^2 in size) and covered an area of 25 km^2. In 1997, a new, larger grid was

established, comprising 32 squares (1 km^2) distributed throughout the GWRA (Månsson et al. 2011). Clusters of pellet plots, each containing 4 10-m^2 sampling plots, were arranged every 200 m along the squares' perimeters. We used the mean pellet count from each cluster in analyses. Following Kjellander (2000) and K. Wallin (Department of Biological and Environmental Sciences, University of Gothenburg, unpublished data), we assumed a defecation rate of 22 pellet groups/deer/day.

We used April surveys as measures of the previous year's deer density in models (Table 1). The current year's deer density also could affect survival rates. However, we estimated deer density after the late winter-early spring period when deaths most commonly occurred. Thus, survival rates should be positively correlated with current density because individuals survived winter to be counted, not because density affected survival. Hence, we considered only the previous year's density in models.

In Bogesund and Grimsö, information on the deer hunted was recorded (sex, ID if marked, and date of death). We calculated the per capita harvest (Table 1) as the number of individuals (marked and unmarked) killed each year, divided by the most recent estimate of deer abundance (based on Sep density surveys in Bogesund and Apr surveys in Grimsö).

Potential Covariates of Roe Deer Survival

Because of the potential for lagged effects on survival, we considered climate and vegetation conditions from the current year (t; overlapping with the year of survival modeled) and the previous year (t-1; Table 1). We obtained climate data at a 0.58 resolution from the Climate Research Unit (CRU) 3.1 dataset (Mitchell et al. 2004, Mitchell and Jones 2005). We extracted the observed climate for the 0.58 cell containing each site and used it to generate climate predictors (Table 1), including winter temperature, winter precipitation, annual precipitation, and annual growing degree days above 58C (Prentice et al. 1992). We calculated mean snow depth (from Nov through Apr following Cederlund 1982) and winter length (Table 1) using data from weather stations near the sites (Ställdalen, 39 km northwest of Grimsö; Stockholm, a few km south of Bogesund; Swedish Meteorological and Hydrological Institute 2015). We calculated annually summarized predictors across the calendar year (Jan–Dec) to allow integration of other climatic datasets, often available on a calendar year basis.

We obtained data on the normalized difference vegetation index (NDVI), a remotely sensed index of vegetation productivity (Running 1990, Field et al. 1995), from the Global Inventory Modelling and Mapping Studies website (http://glcf.umiacs.umd.edu/data/gimms/, accessed 30 Sep 2010) at a 0.078 resolution. We spatially overlaid NDVI data with site polygons and calculated area-weighted means of bimonthly NDVI values for each site. We used annually integrated NDVI (INDVI; Table 1) as an index of annual vegetation production.

Despite their colonization of Grimsö in 2003, wolves were unlikely to be an important influence on deer survival during the modeled period because the first roe deer killed by wolves was recorded in 2006. Consequently, we considered only lynx in our analyses. In Sweden, the number of lynx family groups/ 1,000 km^2 has been estimated since 1994 (Andr_en et al. 2002). We averaged density estimates from 2 neighboring lynx bioregions (16,484 km^2 and 15,872 km^2) to create lynx density estimates for Grimsö (Table 1). We assumed a regional density of 0 lynx families/km^2 prior to 1994. Because tracks of family groups were not observed in Grimsö until 1996, we constructed a binary variable representing lynx presence in the site and inferred local colonization in 1996 (Table 1).

Modeling Methods and Sampling Periods

We modeled survival using 2 contrasting approaches; consistent results from these methods would greatly increase confidence in conclusions. First, beta-binomial and binomial (collectively BB) models estimate survival (S) based on data collated across the entire year. These BB models assume a binomial distribution of errors. The beta-binomial models (not the simple binomial models) contain a parameter to account for extra-binomial variation. Second, capture–mark– recapture (CMR) models used individual capture histories from observations across 2 sub-annual periods. This latter method exploits the fact that deer were individually marked, and estimates annual survival between 3-month-long primary sampling periods in consecutive years. Because the majority of deer observations took place in late winter, we used January through March as the primary period in the CMR models. For comparability, we summarized response data for the BB models from one February to the next. We performed analyses in program R 3.0.2 (R Development Core Team 2013).

For the BB models, we counted each individual once/year and estimated survival (S) from the ratio of dead to total individuals for a year. We used an all subsets approach to model construction: we ran models with all possible 2-variable combinations of the climate, vegetation, density, harvest, and lynx variables. We excluded combinations of strongly correlated variables (Pearson's $r > 0.4$; Freckleton 2011; see Supporting Information, Table S1). We included age group and sex in all models because they have well documented effects on deer survival (Gaillard et al. 1998). We classified individuals as fawns (>3 months and <1 year old), subadults and adults (1–7 years old), or senescents (>7 years old; Gaillard et al. 1993). We calculated Akaike's Information Criterion (AIC) for all models and ranked them according to DAIC and model weight (v_i; Anderson et al. 2000, Burnham and Anderson 2002). We included models with DAIC 6 in the selected model set and excluded models with a greater AIC than simpler, nested alternatives (Richards 2008) to remove uninformative parameters before model averaging (Arnold 2010). We averaged parameters, predictions, and their standard errors from the selected model sets using formulae in Burnham and Anderson (2004). We calculated variable importance as the sum of weights of all models containing that variable.

We evaluated the predictive ability of the BB models by using model likelihoods to calculate each model's pseudo-R^2, R_N^2 (Nagelkerke 1991), a measure of model fit for non-linear models that varies between 0 (explanatory power equivalent to an intercept only model) to 1 (perfect fit). We assessed model robustness to outliers and sample-size with cross-validation. In particular, we excluded 1 year (repeated once for each year) or 5 years (repeated for 1,000 random samples of 5 years) of data from the datasets, re-fitted the model using reduced datasets, and used the model to reproduce the omitted data. We calculated the likelihood of the left-out observations (assuming a binomial error distribution) using estimates from each model and an intercept-only model and used these likelihoods to calculate R_N^2.

Barker models are a form of CMR model that, unlike Cormack–Jolly–Seber models (Cormack 1964, Jolly 1965, Seber 1965), allow the incorporation of dead recoveries and live re-sightings of individuals from open periods in between closed primary sampling periods (hereafter, primary periods). The population is assumed to be closed during the primary period (i.e., no deaths, births, or emigrations). Intervening open secondary periods (hereafter secondary periods) last from the end of one primary period to the beginning of the next and involve no closure assumptions. Barker models estimate several control parameters pertaining to site fidelity (i.e., emigration probability) and observation probabilities during the sampling periods (Barker and Kavalieris 2001). For further description of Barker models see Barker (1997). We compiled live and dead observations into capture histories (1/individual) and modeled survival in Program MARK (White and Burnham 1999).

Our Barker models had 1 3-month-long primary period (Jan-Mar) and 1 9-month-long secondary period (Apr_Dec) per year. We attributed deaths during the primary period to the closest open period. Closed population capture–recapture methods are relatively robust to such violations of closure given that the primary period is short relative to the intervening secondary period (Kendall 1999, Lindberg 2010). These models assume that all marked individuals have the same probability of recapture and survival. We included several covariates to control for possible sources of heterogeneity. First, because radio-collared individuals are more likely to be observed, we included whether an individual was radio-collared as a covariate of 2 control parameters: r (probability of recovering an animal that has died) and R (probability that an animal surviving the secondary period is observed alive). Second, we added constraints to describe site fidelity: the F and F' parameters describe the probability that an individual will emigrate from (1-F) or return to (F') the study site during the secondary period. We considered age as a covariate of F and allowed individuals turning 1 year old during the secondary period to have a separate emigration probability, accommodating the natal dispersal common among subadult roe deer (Gaillard et al. 2008). Finally, we included the number of capture days as a covariate of p (primary period capture probability) to control for variation in trapping effort.

We constructed model sets for Bogesund and Grimsö by including covariates of survival

(S). We ran survival models with all possible combinations 2 predictors, in addition to sex and age group (always included). We did not consider combinations of variables that were strongly correlated (Pearson $r > 0.4$; Table S1). We compared models for each site using AIC and included models with ΔAIC 6 in the selected model sets. We then averaged the parameters, estimates of survival, and associated standard errors from these CMR models (Burnham and Anderson 2004). We compared survival estimates based on each model to the observed survival based on the records of roe deer and their deaths. To evaluate model fit, we calculated the root-mean-square deviance (RMSD) between each model's estimates and the observed survival of all age–sex groups except fawns. The fawn survival represented by the observed data was limited to fawns between 4 months and 12 months of age and did not reflect the period of fawn survival estimated by the CMR models (8–20 months of age).

RESULTS

At Bogesund, there were 1,339 unique live observations across years (1988–1989 to 2005–2006), and 275 death records. At Grimsö, there were 1,449 unique live observations (1984–1985 to 2005–2006), and 319 death records. The CMR models used capture histories of 466 deer in Bogesund and 557 deer in Grimsö. Trapping effort varied across years. At Bogesund, there were an average of 14.6 ± 3.79 (SD) trap locations and 23.0 ± 13.56 unique capture dates from 1988–1989 to 2005–2006. At Grimsö, there were 10.8 ± 1.40 trap locations (1989–1990 to 2005– 2006; earlier data not available) and 24.6 ± 8.92 unique capture dates (1984–1985 to 2005–2006). Strong correlations between variables precluded consideration of 9 variable combinations in Bogesund and 21 in Grimsö (Table S1).

Roe Deer Survival in Bogesund

Of 275 recorded deaths in Bogesund, 96 were human-related including 54 that were harvested. The majority (153) of the remaining deaths were due to starvation. Observed survival rates ranged from 0.47 to 0.96 across years, averaging 0.80 ± 0.034 (SE, n = 18; for age-group and sex-specific rates; Table 2).

Two BB models for Bogesund had DAIC 6 (Table 3). Model-averaged parameters from these 2 models included a strong negative effect of harvest and a positive effect of the previous year's INDVI (Table 4). Survival increased marginally with previous year's precipitation, but the 95% confidence intervals (CI) of the parameter estimate over-lapped 0. The model-averaged survival estimates were similar to the observed survival data (Fig. 2a and b, $R_N^2 = 0.75$). Both selected models had similar explanatory power (R_N^2 of 0.76 and 0.75) and performed well in cross-validation with R_N^2 declining only slightly when we excluded data from model fitting (Table 3).

No models were within ΔAIC ≤ 6 of the highest ranked CMR model (Table 5). Similar to

the BB model, this model included a strong negative relationship between survival and harvest and a positive relationship between survival and the previous year's INDVI (Table 6). The effect sizes of the CMR parameters were generally similar to the modelaveraged BB parameters (Tables 4 and 6). Model estimates of survival closely resembled those of the BB model and observed survival rates (RMSD = 1.33; Fig. 2c and d). The control parameters indicated that log-odds ratio of capture during the primary sampling period increased with trapping effort (0.11 ± 0.032 increase/capture date) and that radio-collared individuals had increased log-odds of observation in the secondary period whether alive (2.32±1.014) or dead (1.75±0.283). The model suggested individuals approximately 1 year old might have a higher emigration probability than older individuals (log-odds of emigration for adults and senescents = -0.31 ± 0.241).

Roe Deer Survival in Grimsö In Grimsö, there were 104 deaths due to harvest and 68 deaths attributed to predation. The majority of the latter (57) were associated with signs of lynx. Observed survival rates were less variable across years in Grimsö (0.78 ± 0.016, n = 22) than in Bogesund (0.80 ± 0.034, n = 18). Survival in Grimsö before 1996 (0.82 ± 0.019, n = 11) was higher than after 1996 (0.74 ± 0.02, n = 11) when lynx were present.

In Grimsö, the selected BB model set included 12 models (Table 3) and the highest ranked model had a weight (v_i) of only 0.32. Lynx presence was included in 10 of the selected models (Table 3). Model-averaged parameter estimates indicated lynx presence reduced roe deer survival by about 11% (relative to mean survival before lynx colonization). Survival increased with the current year's INDVI and, more weakly, with winter temperature and the previous year's density (Table 4). The model-averaged 95% CI of other parameters included in the model set overlapped 0 (annual precipitation, snow depth, winter length, previous year's INDVI; Table 4). Model-averaged estimates captured interannual variation in survival well (Fig. 3a and b, $R_N^2 = 0.67$). Model R_N^2 declined little in cross-validation indicating that predictive ability was robust to exclusion of data from model fitting (Table 3).

In Grimsö, there were 9 CMR models with $\Delta AIC \leq 6$ (Table 5). As in the BB model set, lynx presence was a relatively important predictor with a negative effect on roe deer survival (Table 6). Based on the model-averaged parameter estimate, lynx presence translated to a 5% decrease in survival rates. Other variables in the selected model set included winter length, winter temperature, lynx density, and annual growing degree days above 58 C, but in all cases, the CIs overlapped 0 (Table 6). The control parameters included a positive relationship between probability of capture during the primary sampling period and trapping effort (log-odds 0.06 ± 0.015 increase per capture date). Additionally, radio-collared individuals had increased log-odds of observation in the secondary period (relative to non-collared individuals), whether alive (1.09 ± 0.153) or dead (0.70 ± 0.305). The models suggested 1 year olds had a greater probability of emigrating than older individuals (log-odds of emigration for adults and senescents = -1.99 ± 0.510). Although the CMR survival estimates were noticeably lower than the BB

estimates and the observed survival rates (Fig. 3), they produced similar trajectories for survival over time (Fig. 3c; RMSD = 1.06).

DISCUSSION

It is important to consider direct climatic, indirect climatic, and non-climatic influences simultaneously when building predictive models of variation in ungulate survival. Many studies of climate impacts do not explicitly consider relatively non-climatic and indirect climatic factors (e.g., predation, food resources; Gilman et al. 2010, Zarnetske et al. 2012). Although we found support for direct climatic effects (e.g., winter conditions in Grimso€), direct climatic predictors were often out-performed by predictors that could be considered representative of indirect climatic or non-climatic effects consistent with past studies of roe deer ecology, which emphasize lagged cohort effects on survival (Gaillard et al. 1998, Pettorelli et al. 2002). Net primary production has previously been positively related to spatial variation in roe deer density and population growth (Melis et al. 2009, 2010) and our results suggest that temporal variation in NPP could affect roe deer survival within sites, thus, influencing population growth. Climate-driven changes in vegetation production, thus, represent an important indirect route via which climate change could affect roe deer.

The selected model sets for Bogesund and Grimsö suggested a few alternative climate-related predictors of roe deer survival. However, these alternatives generally received less statistical support than INDVI and may also affect deer via food availability. For example, higher precipitation could contribute to increased vegetation production (Lieth and Whittaker 1975). In Bogesund, substituting precipitation with INDVI as a predictor increased model performance suggesting the value of including vegetation metrics directly. In Grimsö, the inclusion of winter temperature, snow depth, and winter length in models could indicate impacts on the energy needed for deer to maintain their body temperature and find food (Cederlund 1982, Parker et al. 1984, Mysterud et al. 1997, Shrestha et al. 2012). Shorter winters could be linked to longer growing seasons and increased vegetation production as supported by the correlation between winter temperatures and INDVI (Table S1). Ultimately, all of these climatic predictors could indicate the same positive relation- ship between vegetation and roe deer survival, which might be better represented by a direct measure of vegetation productivity.

Non-Climatic Effects: Predation and Human Harvest

Our results provide strong evidence for the importance of non-climatic influences on roe deer mortality in both sites: human harvest in Bogesund and lynx presence in Grimsö. Useful projections of roe deer population dynamics in these areas must include these factors. Harvest by humans was a nearly constant source of mortality in Bogesund because of the extensive management of this population for research purposes. In Grimsö, where lynx are present and the deer population has not been heavily managed, it is, perhaps, unsurprising that predictors related to lynx predation took on a central role.

The 5–11% decrease in roe deer survival associated with lynx presence was similar to that observed after lynx re-colonization of a site in Germany ($10%; Heurich et al. 2012). Populations of lynx and wolves are recovering in many parts of Europe and North America (Linnell et al. 2000, Mech and Boitani 2003, Beschta and Ripple 2009). These results further emphasize that the understanding of ungulate populations and their responses to imminent environmental change would be improved by examining more datasets from sites with natural predators (Gaillard et al. 2000b, Nilsen et al. 2009a).

The considerable uncertainty in model selection for Grimsö suggests caution when interpreting the effect of (e.g., INDVI, harvest, predation). Despite some variation in results between modeling methods, the BB and CMR models for Grimsö and Bogesund generally identified non-climatic and indirect climatic variables (e.g., lynx presence, harvest, INDVI) as of greatest importance. At Bogesund, results were consistent across methods; harvest and INDVI were important predictors of survival regardless of modeling technique. In Grimsö, both methods emphasized the impact of lynx but gave different results for climatic effects, highlighting the potential for these methods to yield slightly different conclusions regarding roe deer survival.

INDVI and Indirect Climatic Effects on Survival

Analyses suggested that INDVI was an important predictor with similar positive effects on roe deer survival in Bogesund and Grimsö. Increased vegetation production could allow individuals to increase growth rates and add to fat reserves, enabling higher rates of survival through the following year. The lagged effect of INDVI in Bogesund is lynx presence; however, several points provide reassurance that the observed relationship is not spurious. First, the effect size of lynx presence is consistent with the weaker negative effect of lynx density when included in models. Second, both modeling methods led to highest-ranked models including lynx presence, whereas for Bogesund, a nearby site without predators, lynx-related predictors were not selected. Third, investigations of variables correlated with lynx presence (e.g., harvest; Table S1) did not reveal alternative explanations for the decrease in roe deer survival observed during this study.

Implications for Roe Deer Population Dynamics Under Climate Change

The survival models presented here indicate that roe deer survival is most likely to be affected by climate changes indirectly via changes in vegetation production. This highlights the need for mechanistic models of the temporal relationship between climate and vegetation. Temperatures and precipitation are expected to increase dramatically in northern Europe over the next century (Fronzek and Carter 2007, Intergovernmental Panel on Climate Change 2007). There is evidence that such changes have already caused a 6% increase in net primary productivity globally (estimated using NDVI; Nemani et al. 2003) and further increases are expected throughout much of Europe including Scandinavia (Slayback et al. 2003, Boisvenue and Running 2006, Fronzek and Carter 2007). To our knowledge, however, projections of primary productivity under climate

change are not available at a temporal resolution (e.g., annual) adequate for modeling consumer population dynamics. Adaptive wildlife management could benefit from models of generally applicable vegetation indices in response to interannual changes in climate.

Given the relationships we identified, climate change is likely to have indirect positive impacts on roe deer survival through increased vegetation production in Bogesund and Grimsö. Similar impacts could be observed in other areas of northern Europe. In both sites roe deer survival rates were generally high but within the range of those observed in other populations. Adult females had an average survival of 0.82 ± 0.036 (SE) in Bogesund and 0.80 ± 0.012 in Grimsö, compared with a range of 0.68–0.99 across other studies (Fruzinski and Labudzki 1982, Gaillard et al. 1993, Cobben et al. 2009, Nilsen et al. 2009a). Ultimately, however, survival rate is only 1 factor contributing to population growth. Recent research has indicated the potential for climate change to have negative effects on roe deer recruitment due to the increasingly early onset of spring (Gaillard et al. 2013). Models describing the factors affecting other vital rates (e.g., fecundity) are needed to investigate how a changing climate will translate into the future dynamics of these populations.

Recovering predator populations add further complexity to projections of future roe deer populations. Increases in survival due to increased vegetation productivity could, at least in part, be ameliorated by increased predation. However, despite the evidence we provide that lynx currently reduce roe deer survival, predicting the role that lynx might play in the future requires caution. Decreases in snowfall associated with climate change may reduce lynx hunting effectiveness and could lead to a decline in lynx abundance, as has been suggested for North America (Carroll 2007). We could not address the potential for climate change to alter lynx-roe deer interactions, but this could provide a fruitful avenue for future work.

MANAGEMENT IMPLICATIONS

Increases in roe deer survival due to heightened vegetation production could be undesirable because of the negative impacts of deer including damage to forestry and crops. Our results suggest that in Sweden, increased harvests and

predation due to recovering predator populations might mitigate increases in roe deer survival rates related to climate-related vegetation changes. However, the future recovery of predator populations is dependent on environmental conditions and government regulation. Managers in areas with few predators may need to further intensify harvest efforts if they desire to reduce climate-related increases in roe deer survival.

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Table 1. Potential covariates of roe deer survival in Sweden, 1985–2006.

Metric	Sample dates[a]	Description
Survival	15 Feb Year$_t$ to 14 Feb Year$_{t+1}$	Dates delineating the effective survival period are approximate. The estimation of survival and the definition of relevant period depends on the type of model used (binomial vs. capture–mark–recapture).
Climate and vegetation predictors		
Annually summarized		
Annual integrated NDVI	Jan Year$_t$ to Dec Year$_t$	Sum of monthly NDVI[b] in calendar year overlapping survival period.
	Jan Year$_{t-1}$ to Dec Year$_{t-1}$	Sum of monthly NDVI in calendar year preceding survival period.
Annual precipitation	Jan Year$_t$ to Dec Year$_t$	Sum of monthly precipitation in calendar year overlapping survival period.
	Jan Year$_{t-1}$ to Dec Year$_{t-1}$	Sum of monthly precipitation in calendar year preceding survival period.
Annual growing degree days	Jan Year$_t$ to Dec Year$_t$	Sum of growing degree days (>5 °C) in calendar year overlapping survival period.
	Jan Year$_{t-1}$ to Dec Year$_{t-1}$	Sum of growing degree days (>5 °C) in calendar year preceding survival period.
Seasonally summarized		
Winter temperature	Dec Year$_{t-1}$ to Feb Year$_t$	Mean monthly daily average temperature in winter preceding survival period.
Winter precipitation	Dec Year$_{t-1}$ to Feb Year$_t$	Sum of precipitation in winter months preceding survival period.
Snow depth	Nov Year$_{t-1}$ to Apr Year$_t$	Mean daily snow depth in cold season overlapping start of survival period.
Winter length	Autumn Year$_{t-1}$ to Spring Year$_t$	Log number of days between first and last snowfall during the cold season overlapping the start of the survival period
Other predictors		
Roe deer density	Apr Year$_{t-1}$	Density from Apr of year prior to survival year being modeled.
Per capita harvest	Aug Year$_t$ to Jan Year$_{t+1}$	No. deer harvested divided by the most recent deer abundance estimate.
Lynx family density	Feb Year$_t$	Density of lynx families (regional surveys) in winter at beginning of survival period.
Lynx presence	Jan Year$_t$ to Dec Year$_t$	Inferred from regional family density and signs in study site.

[a] Unless otherwise stated sample dates given are inclusive of start and end months. The subscript *t* following Year denotes any given year during the study period for each site.
[b] Normalized difference vegetation index is abbreviated NDVI.

Table 2. Observed and model estimated survival rates of roe deer among age groups and sexes in Bogesund (1989–2006) and Grimsö (1985–2006), Sweden.

		Fawn survival (SE)[b]		Adults and subadult survival (SE)		Senescent survival (SE)	
Site	**Estimate source**[a]	**F**	**M**	**F**	**M**	**F**	**M**
Bogesund	Observed	0.80 (0.05)	0.80 (0.05)	0.82 (0.04)	0.82 (0.04)	0.72 (0.04)	0.52 (0.12)
	BB model	0.81 (0.03)	0.79 (0.03)	0.83 (0.03)	0.81 (0.03)	0.65 (0.04)	0.62 (0.04)
	CMR model	0.68 (0.03)	0.63 (0.03)	0.82 (0.02)	0.78 (0.02)	0.59 (0.03)	0.54 (0.03)
Grimsö	Observed	0.95 (0.02)	0.92 (0.03)	0.80 (0.01)	0.67 (0.03)	0.54 (0.06)	0.46 (0.14)
	BB model	0.95 (0.00)	0.91 (0.01)	0.79 (0.01)	0.67 (0.02)	0.62 (0.02)	0.47 (0.02)
	CMR model	0.67 (0.01)	0.54 (0.01)	0.75 (0.01)	0.64 (0.01)	0.57 (0.01)	0.43 (0.01)

[a] Observed denotes the observed survival rates calculated based on the records of roe deer and their deaths, BB model denotes use of model-averaged parameter estimates from the selected best binomial and beta-binomial models, and CMR model denotes use of model-averaged parameter estimates from the selected best capture–mark–recapture models.

[b] The values shown represent the mean and standard error of the estimated survival rates across the years modeled in each site (Bogesund, $n = 18$ years; Grimsö, $n = 22$ years).

Table 3. Binomial and beta-binomial models of roe deer survival in Bogesund, Sweden, 1989–2006 ($n = 103$), and Grimsö, Sweden, 1985–2006 ($n = 119$). We ranked models using Akaike's Information Criterion (AIC) with each model's Akaike weight denoted by ω_i (among models with ΔAIC ≤ 6) and number of parameters denoted by K. R_N^2 is Nagelkerke's approximation of R^2. Cross-validation was conducted by excluding 1 or 5 years of data before refitting the model, predicting survival in excluded years and estimating R_N^2 for these predictions.

						Cross-validation R_N^2	
Survival (S) ~[a]	**Model type[b]**	**K**	**ΔAIC**	**ω_i**	**R_N^2**	**1 year**	**5 years**
Bogesund							
Age, sex, harvest$_t$, INDVI$_{t-1}$	Beta-bin	7	0.00	0.88	0.76	0.75	0.73
Age, sex, harvest$_t$, precipitation$_{t-1}$	Beta-bin	7	4.00	0.12	0.75	0.74	0.72
Age, sex	Beta-bin	5	49.31	0	0.61	0.64	0.63
Null model (intercept-only)	Beta-bin	2	57.76	0	0.55	0.60	0.61
Age, sex	Bin	4	112.39	0	0.19	0.08	0.06
Null model	Bin	1	128.08	0	0	0	0
Grimsö							
Age, sex, lynx presence$_t$, INDVI$_t$	Bin	6	0.00	0.32	0.70	0.68	0.68
Age, sex, lynx presence$_t$, INDVI$_{t-1}$	Beta-bin	7	2.05	0.12	0.69	0.67	0.67
Age, sex, roe deer density$_{t-1}$, winter temperature$_t$	Beta-bin	7	3.01	0.07	0.69	0.67	0.67
Age, sex, lynx presence$_t$, INDVI$_{t-1}$	Bin	6	3.02	0.07	0.69	0.66	0.65
Age, sex, lynx presence$_t$, precipitation$_{t-1}$	Beta-bin	7	3.14	0.07	0.69	0.67	0.68
Age, sex, lynx presence$_t$, snow depth$_t$	Beta-bin	7	3.34	0.06	0.69	0.67	0.66
Age, sex, lynx presence$_t$	Beta-bin	6	3.44	0.06	0.68	0.67	0.67
Age, sex, roe deer density$_{t-1}$, winter temperature$_t$	Bin	6	3.46	0.06	0.69	0.67	0.66
Age, sex, lynx presence$_t$, snow depth$_t$	Bin	6	3.80	0.05	0.69	0.66	0.66
Age, sex, lynx presence$_t$, precipitation$_{t-1}$	Bin	6	3.90	0.05	0.69	0.67	0.66
Age, sex, lynx presence$_t$, winter length$_t$	Bin	6	3.99	0.04	0.69	0.66	0.66
Age, sex, lynx presence$_t$	Bin	5	4.33	0.04	0.68	0.66	0.66
Age, sex	Beta-bin	5	19.34	0	0.63	0.62	0.62
Age, sex	Bin	4	23.13	0	0.62	0.60	0.60
Null model (intercept-only)	Beta-bin	2	95.77	0	0.23	0.24	0.24
Null model	Bin	1	128.01	0	0	0	0

[a] Age (3 groups: fawns, subadults and adults, and senescents) and sex were categorical variables. Harvest rates, lynx presence, winter temperature, snow depth, and winter length are from the current year (t). Precipitation metric and roe deer density were from the previous year ($t-1$). Annually integrated normalized difference vegetation index (INDVI) was from either the current (t) or previous year ($t-1$).

[b] Beta-binomial (Beta-bin) models contain an extra parameter that accounts for over-dispersion in the data that is not accounted for by binomial (Bin) models. Null models include only an intercept and, for beta-binomial models, the over-dispersion parameter.

Table 4. Binomial and beta-binomial coefficients of roe deer survival in Bogesund, Sweden, 1989–2006 ($n = 103$), and Grimsö, Sweden, 1985–2006 ($n = 119$). We ranked models using Akaike's Information Criterion (AIC). Model-averaged coefficients are presented along with their standard errors and 95% confidence intervals across all binomial and beta-binomial models with Δ AIC ≤6. Variable importance is the sum of Akaike weights of all models with ΔAIC ≤6 containing that variable.

Parameter[a]	Estimate	SE	LCL	UCL	Variable importance
Bogesund					
Intercept (adult F)	−7.78	3.699	−15.03	−0.53	1.00
Age: fawn	−0.17	0.214	−0.60	0.255	1.00
Age: senescent	−1.10	0.235	−1.56	−0.64	1.00
Sex: M	−0.15	0.182	−0.51	0.21	1.00
Harvest_t	−3.98	0.535	−5.03	−2.93	1.00
INDVI_{t-1}	1.08	0.268	0.55	1.60	0.88
$\text{Precipitation}_{t-1}$	0.01	0.002	0	0.01	0.12
Grimsö					
Intercept (adult F)	−0.87	3.517	−7.76	6.02	1.00
Age: fawn	1.62	0.218	1.19	2.04	1.00
Age: senescent	−0.87	0.227	−1.31	−0.43	1.00
Sex: M	−0.63	0.144	−0.91	−0.35	1.00
Lynx presence_t	−0.62	0.152	−0.92	−0.32	0.87
INDVI_t	0.45	0.183	0.10	0.81	0.32
INDVI_{t-1}	0.37	0.204	−0.03	0.77	0.19
$\text{Roe deer density}_{t-1}$	0.01	0.003	0.01	0.02	0.13
$\text{Winter temperature}_t$	0.09	0.036	0.02	0.16	0.13
$\text{Precipitation}_{t-1}$	−0.001	0.0008	−0.003	0.0003	0.11
Snow depth_t	−0.01	0.009	−0.03	0.004	0.11
Winter length_t	−0.75	0.497	−1.72	0.222	0.04

[a] Age (3 groups: fawns, subadults and adults, and senescents) and sex were categorical variables. Harvest rates, lynx presence, winter temperature, snow depth, and winter length are from the current year (t). Precipitation metric and roe deer density were from the previous year ($t-1$). Annually integrated normalized difference vegetation index (INDVI) was from either the current (t) or previous year ($t-1$).

Table 5. Capture–mark–recapture models of roe deer survival in Bogesund, Sweden, 1989–2006 ($n = 1{,}066$) and Grimsö, Sweden, 1985–2006 ($n = 1{,}250$). We ranked models using Akaike's Information Criterion (AIC) with each model's Akaike weight denoted by ω_i (among models with $\Delta AIC \leq 6$) and number of parameters denoted by K. RMSD is the root-mean-square deviance between each model's estimates and the observed survival of all age–sex groups except fawns.

Survival (S) $\sim$[a,b]	K	ΔAIC	ω_i	RMSD
Bogesund				
Age, sex, harvest$_t$, INDVI$_{t-1}$	13	0.00	1	1.33
Age, sex	11	55.63	0	1.66
Control model	8	91.09	0	1.77
Null model	5	176.81	0	1.76
Grimsö				
Age, sex, lynx presence$_t$, winter length$_t$	16	0.00	0.30	1.05
Age, sex, lynx presence$_t$, winter temperature$_t$	16	1.49	0.14	1.06
Age, sex, lynx presence$_t$	15	1.93	0.11	1.06
Age, sex, lynx density$_t$, winter length$_t$	16	1.99	0.11	1.08
Age, sex, lynx density$_t$, winter temperature$_t$	16	2.61	0.08	1.08
Age, sex, growing degree days$_t$, winter temperature$_t$	16	2.86	0.07	1.08
Age, sex, lynx density$_t$	15	3.15	0.06	1.08
Age, sex, winter temperature$_t$	15	3.37	0.06	1.11
Age, sex	14	4.36	0.03	1.12
Control model	11	32.39	0	1.33
Null model	7	127.55	0	1.34

[a] The capture–mark–recapture model used, a Barker model, includes 6 parameters (p, F, F', r, R, R'), other than S (survival). Covariates for these control parameters were included to control for heterogeneity in the data. Capture effort (no. capture days) was included as a covariate of p, radio-collared status as a covariate of r and R, and age (only 2 groups considered: fawns vs. >1 year olds) as a covariate of F. These covariates were consistent across models. The control model (listed for comparison) included these covariates, but included no predictors of survival (S). The null model included only intercepts for all parameters.

[b] Age (3 groups: fawns, subadults and adults, and senescents) and sex were categorical variables. Harvest rates, lynx presence, winter length, winter temperature, lynx density, and growing degree days are from the current year (t). Annually integrated normalized difference vegetation index (INDVI) was from the previous year ($t-1$).

Table 6. Capture–mark–recapture coefficients of roe deer survival in Bogesund, Sweden, 1989–2006 ($n = 1{,}066$) and Grimsö, Sweden, 1985–2006 ($n = 1{,}250$). We ranked models using Akaike's Information Criterion (AIC). Model-averaged coefficients along with their standard errors and 95% confidence intervals across all capture–mark–recapture models with ΔAIC ≤6 are presented for Grimsö. For Bogesund, there was only one model with ΔAIC ≤6 so coefficients along with their standard errors and 95% confidence intervals from that model are presented. Variable importance is the sum of Akaike weights of all models with ΔAIC ≤6 containing that variable.

Parameter[a]	Estimate	SE	LCL	UCL	Importance
Bogesund					
Intercept (adult F)	−7.90	1.968	−11.76	−4.04	1.00
Age: fawn	0.80	0.169	0.47	1.13	1.00
Age: senescent	−0.40	0.231	−0.86	0.05	1.00
Sex: M	−0.21	0.131	−0.46	0.05	1.00
Harvest_t	−2.66	0.388	−3.42	−1.90	1.00
INDVI_{t-1}	0.88	0.195	0.50	1.26	1.00
Grimsö					
Intercept (adult F)	2.97	2.800	−2.52	8.45	1.00
Age: fawn	0.40	0.174	0.06	0.74	1.00
Age: senescent	−0.44	0.263	−0.96	0.07	1.00
Sex: M	−0.54	0.127	−0.79	−0.29	1.00
Lynx presence_t	−0.31	0.141	−0.59	−0.03	0.55
Winter length_t	−0.93	0.490	−1.89	0.03	0.41
$\text{Winter temperature}_t$	0.05	0.030	−0.01	0.11	0.35
Lynx density_t	−0.10	0.053	−0.20	0.01	0.25
$\text{Growing degree days}_t$	−0.001	0.0004	−0.002	0.0002	0.07

[a] Age (3 groups: fawns, subadults and adults, and senescents) and sex were categorical variables. Harvest rates, lynx presence, winter length, winter temperature, lynx density, and growing degree days are from the current year (t). Annually integrated normalized difference vegetation index (INDVI) was from the previous year ($t-1$).

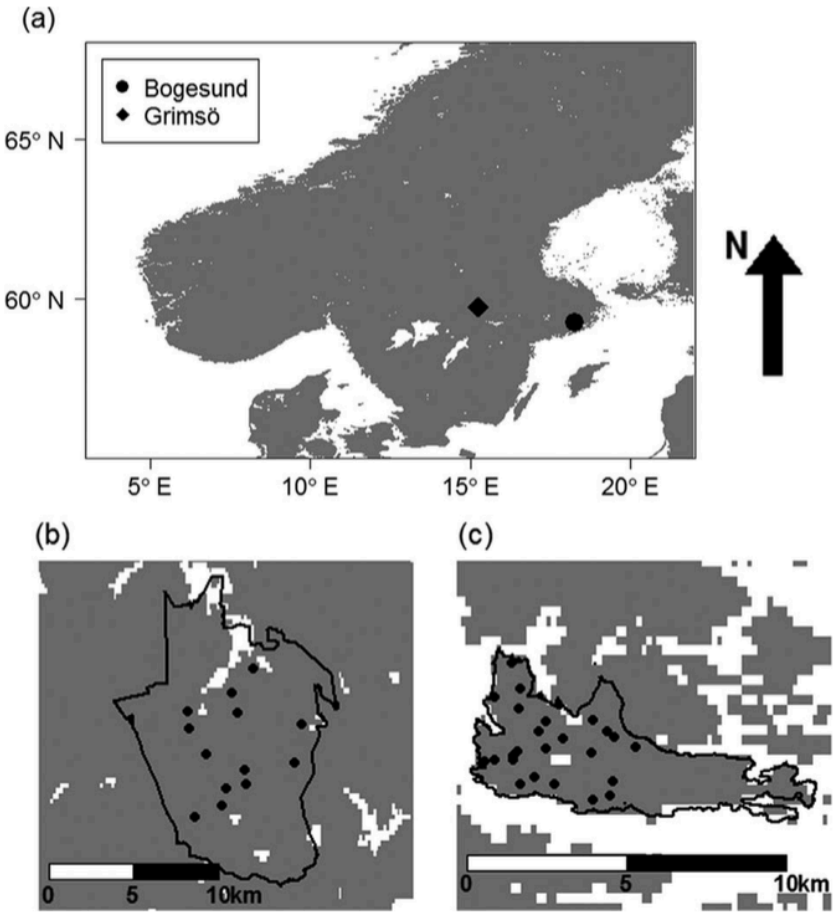

Figure 1. Grimsö and Bogesund are located approximately 150 km apart in southeastern Scandinavia (a). The outlined areas represent the boundaries of the Grimsö Wildlife Research Area (GWRA; b) and the Bogesund peninsula (c). The box-trap grids (points) in Grimsö and Bogesund include sub-portions of these areas of approximately 80 km^2 and 12.5 km^2 (also known as the X-area within Bogesund), respectively, defining the study sites. White areas represent inland lakes and ponds (b), and the Baltic Sea (c).

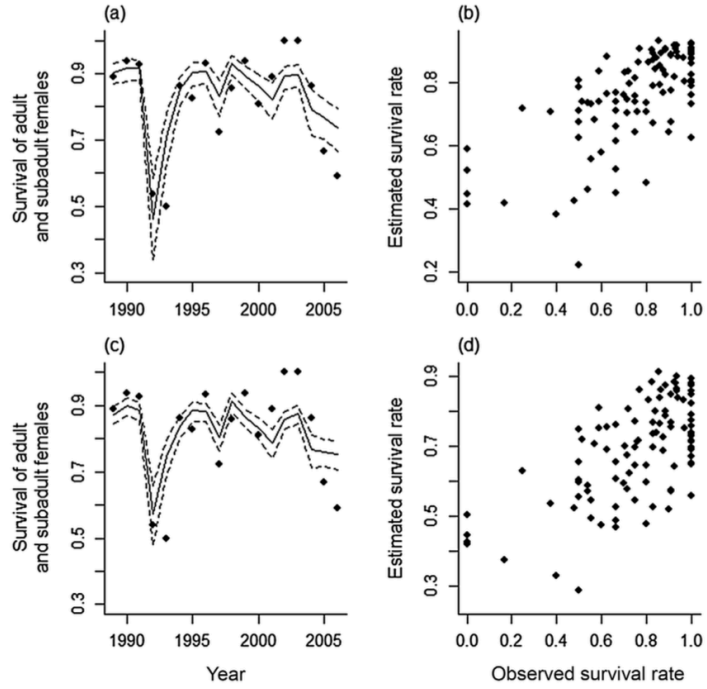

Figure 2. Performance of selected models of roe deer survival in Bogesund, Sweden, was evaluated by comparing model-averaged estimates with observed survival rates. The time-series of observed (points) and estimated (solid lines with dashed lines indicating 95% CIs) survival rates of adult and subadult females are shown for the beta-binomial and binomial models (BB; a) and capture–mark–recapture models (CMR; c). The relationship between observed and estimated survival rates of all age and sex groups for all years of the study period (1989–2006) is shown for the BB (b) and CMR models (d).

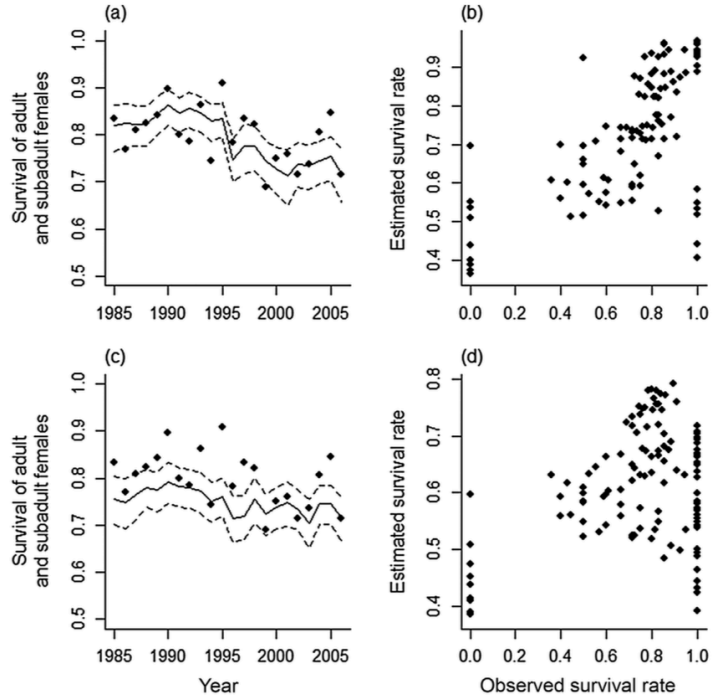

Figure 3. Performance of selected models of roe deer survival in Grimsö, Sweden, was evaluated by comparing model-averaged estimates with observed survival rates. The time-series of observed (points) and estimated (solid lines with dashed lines indicating 95% CIs) survival rates of adult and subadult females are shown for the beta-binomial and binomial models (BB; a) and capture–mark–recapture models (CMR; c). The relationship between observed and estimated survival rates of all age and sex groups for all years of the study period (1985–2006) is shown for the BB (b) and CMR models (d).